LII.—*Contributions to the Development of the Tooth-Rudiments in Rodents.* By Paul Freund *.

In the autumn of 1890, at the suggestion of Prof. Born, I commenced to investigate the development of the dentition of various Rodents, with a view to discovering whether in the diastema between the fully developed teeth it was still possible to find remains of rudiments of such as had disappeared. It was only after making certain discoveries bearing upon the question that I learnt that a paper by MM. Pouchet and Chabry † contains a series of statements with reference to this subject. Nevertheless, when I have furnished a more precise critical comparison of the results of these authors with my own, it will be seen that what are really very material points have escaped their notice.

The dentition of the Rodents attracts attention in the first place owing to the great reduction in the number of the teeth. The largest number is found in the Leporidæ, which possess twenty-eight teeth, namely $i.\ \frac{2}{1}$, $c.\ \frac{0}{0}$, $m.\ \frac{6}{5}$, the smallest in the Muridæ, in which in the majority of cases the number is sixteen, namely $i.\ \frac{1}{1}$, $c.\ \frac{0}{0}$, $m.\ \frac{3}{3}$; while in *Hydromys* we actually find only twelve teeth ($i.\ \frac{1}{1}$, $c.\ \frac{0}{0}$, $m.\ \frac{2}{2}$). The incisors are always separated by a wide diastema from the molars or premolars, as the case may be. As further peculiarities we must regard the absence of the milk-dentition in many species and also the circumstance that the incisors invariably, and the molars usually, belong to the category of continually growing rootless teeth.

It is assumed by all authors who have written concerning the origin of the Rodents that the latter have been derived from forms with a fuller and, above all, more completely equipped dentition, and that consequently the reduction in the number and the disappearance of certain kinds of teeth, such as the canines, are phenomena of a secondary character, connected with the special adaptation of the dentition to a peculiar sort of food, which could hardly be turned to account without this modification of the teeth. In other words, the

* Translated from the 'Archiv für mikroskopische Anatomie,' Bd. 39, pp. 525–554 (Bonn, 1892): from a separate impression communicated by Dr. Forsyth-Major.

† G. Pouchet and L. Chabry, "Contributions à l'Odontologie des Mammifères," Journal de l'Anatomie et de la Physiologie: Paris, 1884.

reduction in the number of the incisors (in the mandible there is always only one on each side, in the upper jaw there are two in the Leporidæ only, in all other cases there is likewise one) and the disappearance of the canines, and, at any rate, of a portion also of the premolars, are related to the modification of the persisting incisors to form chisel-like gnawing-teeth, by means of which the animals are able to consume even very solid vegetable food-substances, such as the bark of trees and grains, the latter of which possess an especially high nutritive value. It has already been demonstrated by numerous authors that the peculiarity of the continuous growth of the gnawing-teeth also belongs to the complete efficiency of the entire arrangement. The effectiveness of this form of dentition in the struggle for existence is at once evident from the great wealth of species possessed by the order Rodentia, the universal geographical distribution of its representatives, as well as the enormous number of individuals composing the various species. The latter phenomenon naturally results from the proverbial fertility of the Rodents; but this, as we know, is directly proportional to the abundance of food and the ease with which it is obtained. It is characteristic that the advantages in the struggle for existence, which are ultimately occasioned by the form of the dentition, are so great that Nature has almost entirely dispensed with the additional gift of other means of defence. The Rodents are among the most defenceless of Mammals.

Our views as to the reduction of the dentition in particular depend upon the conceptions which we have formed as to the phylogenetic derivation of the Rodents. A whole series of such conceptions, however, have already been formulated by various authors. The fullest and most recent treatment of this subject, which is based upon an exhaustive comparison of the dentition, of various parts of the skeleton, the urogenital system, and the mammary organs, is furnished by A. Fleischmann *.

Fleischmann is inclined to derive the Rodents from marsupial-like ancestors, with a complete insectivorous dentition. In his seventh chapter, which he terms a "Phylogenetic Sketch," he sums up his results as follows:—"In the organization of the Rodents two different stages are accordingly recognizable, which are full of meaning for the history of Mammals. On the one side many peculiarities are emphasized which are of functional importance in a lower stage,

* 'Embryologische Untersuchungen von A. Fleischmann, Privatdocent in Erlangen,' ii. Heft.: A. "Die Stammesgeschichte der Nagethiere."

represented by the Marsupialia; on the other many conditions of form are approximated to the type of the higher Placentalia. The Rodents stand as it were as ancient monuments of a time which has long since disappeared, and unfold before us the representation of the modification which, perhaps as early as the Cretaceous period, elevated the Protheria into the condition of placental Mammals. Nevertheless the facts with which we are at present acquainted do not suffice to prove a direct relationship to the Marsupials. **It is only possible to maintain that animals very similar in their organization to the structure of the Marsupialia were the ancestors of the Rodents.** The forms of phylogenetic importance are not concentrated in one group, but are distributed over all four divisions of the Rodentia; for, in accordance with the special conditions of existence, with which we are still very imperfectly acquainted, certain organs have retained their primitive characters in one division, and others in another." In direct reference to our results in the case of *Lepus* I would also like to quote here the concluding sentence of the same chapter:—"As regards the Lagomorpha, it seems to me that the theory founded by Schlosser is established, namely that they did not branch off from the primitive stock simultaneously with the true Rodents, but that they have existed as placental Rodents only for a relatively short period."

In other respects Schlosser's admirable palæontological and general investigations* upon the organization and historical development of the Rodents have already been exhaustively discussed in Fleischmann's treatise.

Especial stress must also be laid upon the fact that, although certain of the herbivorous Marsupials possess a dentition which is in the highest degree similar to that of the Rodents (*Phascolomys* even has continuously growing incisors, and withal the dental formula $i.\ \frac{1}{1}, c.\ \frac{0}{0}, p.\ \frac{1}{1}, m.\ \frac{4}{4}$), Fleischmann nevertheless expresses himself very decidedly against a direct derivation of the Rodents from these animals. He writes:—"The herbivorous Marsupials do not stand in a closer phylogenetic relation to the Rodents, but are a peculiarly differentiated branch of the Metatheria. My object in minutely describing the dentition of various Marsupialia was merely to demonstrate that the reduction of an originally complete dentition in the herbivorous Diprotodontia occasions arrangements which are very similar to the dentition of the

* M. Schlosser, "Die Nager des europäischen Tertiärs nebst Betrachtungen über die Organisation und die geschichtliche Entwicklung der Nager überhaupt": Cassel, 1885. 'Palæontographica,' 31 Bd. Dritte Folge, 7 Bd.

Rodents. Consequently, if in a branch of the Mammalian stem it is possible to recognize in actual examples the development of an upper and lower pair of incisors, accompanied by the loss of the rest of the incisors and the canines, it is also a probable assumption that in the ancestors of the Rodents a similar process occasioned an analogous result. In the group which was undergoing modification the adaptation of the cutting-teeth to their heightened function would have advanced further, since the rooted incisors attained a prismatic shape and the faculty of permanent regeneration."

Another view is supported by Cope *, who derives the Rodents from the Bunotheria, as represented by the suborder Tillodontia, which, while possessing a more complete dentition, exhibit a decided rodent-like formation of individual incisors.

With reference to the results of our embryological investigations, it seems worth remarking that, according to this derivation, the large gnawing-teeth of the existing Rodentia would correspond to the second incisors of what Cope supposes to have been their ancestors, since in the latter the first incisor is already rudimentary and small, while the second is developed into the gnawing-tooth.

An altogether separate position is taken up by Baume † in his speculations.

This position is in the first place based upon the fact that this author is desirous of regarding continuously growing teeth as the prototypes of Mammalian teeth in general. In forming this conception he relies upon the view that the continuously growing rootless tooth is of relatively simpler construction. At the same time he considers that the organization of such teeth is adapted for the production of a mass of tooth-substance. This property is likewise considered by Baume to be of a primitive character, since, as he urges, in the whole animal series we may recognize the law of a progressive reduction in the formation of tooth-substance. Moreover, according to Baume, with the exception of the Rodentia, animals with continuously growing teeth belong to old groups, the still existing representatives of which are perhaps on the way to extinction. It is evident that by

* Cope, "The Mechanical Causes of the Development of the Hard Parts of the Mammalia," Journ. of Morphology, vol. iii. 1889 (Boston). I was unfortunately unable to consult the actual original communications of this author upon the present subject in the 'American Naturalist' of 1883–84 and the 'Report of the United States Geological Survey.—Tertiary Vertebrata,' 1885.

† R. Baume, 'Odontologische Forschungen, Theil i.—Versuch einer Entwicklungsgeschichte des Gebisses': Leipzig, 1882.

adopting Baume's view we avoid a difficulty of the following kind: if we derive continuously growing rootless teeth from rooted teeth with limited growth, we are compelled to assume a repetition of the same process (convergence) in representatives of the most widely different families, which have no direct connexion whatever one with another; for, according to Baume, we find continuously growing teeth "in a motley series among the Carnivora, Cetacea, Prosimiæ, Multiungulata, Sirenia, Ruminantia, Rodentia, and Marsupialia. They are, as appears from the above comparison, widely distributed, but also very scattered, when relationships are considered. The various representatives occupy a number of isolated positions."

Mahn * and Fleischmann have disputed the justice of Baume's assumptions, adducing weighty arguments in opposition to them.

Moreover this conception of Baume's is in accordance with the other peculiar views advanced by this author, the most prominent of which is his theory that the milk-teeth should not be regarded as constituting a special dentition. According to this idea we should only get a pseudo-diphyodontism in Mammals. The milk-teeth would belong to the same series as the permanent ones; they would merely be feebler structures, developing more quickly. The stronger (permanent) teeth develop more slowly according to Baume, but afterwards displace the quickly developed feeble (milk-) teeth. This is not the place for the elucidation of the question as to what are the facts of comparative anatomy and embryology upon which Baume bases his conception. I still have to refer incidentally in the special portion of this paper to the results of Baume's investigations into ontogeny. At any rate, even Baume coincides with all other authors in assuming that the dentition of the Rodentia has arisen by means of reduction from a richer and completer series of teeth.

How extensive the reduction must be supposed to have been is evident from a comparison of the existing dental equipment of the Rodents with the fundamental type of the dentition of the Eutheria, as the latter is formulated by Schlosser † after Oldfield Thomas. According to the theory referred to, the ancestors of the Placentalia would have possessed five incisors, one canine, four premolars, and four molars, though it must certainly be remarked that such an

* R. Mahn, "Bau und Entwicklung der Molaren bei *Mus* und *Arvicola*," Morphol. Jahrb. Bd. xvi. Heft 4.

† M. Schlosser, "Ueber die Deutung des Milchgebisses der Säugethiere," Biol. Centralbl. Bd. x.

abundance of teeth is not found to be realized in any recent or known fossil form.

The question now arises as to how far traces of the process of reduction, and remnants of the teeth which have disappeared, still admit of embryological demonstration in the case of the Rodents.

This query naturally further divides itself into three in the following manner, each of which questions must be separately investigated for the upper and lower jaw :—

(1) Since, with the exception of the premaxilla of the Leporidæ (in which two teeth are present), the recent Rodentia possess only one incisor, we are confronted with the question whether vestiges of the other incisors which have disappeared are traceable in the embryo. Herein, especially in connexion with the views of Cope which have been mentioned above, regard must be paid to the position of possible embryonic rudiments with reference to the large incisor. Are the rudiments situated on the inside or outside of the latter? And is this consequently to be considered as *i.* 1 or as *i.* 2?

(2) Do vestiges of tooth-rudiments exist in the diastema? This question divides itself, according to the three stages which are observable in the embryonic development of teeth, into three subquestions :—

(*a*) Do we find only a dental fold (Zahnleiste) in the diastema?

(*b*) If such a structure is present, are enamel-organs formed upon it?

(*c*) Is enamel produced within the enamel-organs, and dentine by the papillæ?

In the event of (*b*) and (*c*) being answered in the affirmative, this supplementary question arises:

Are the tooth-rudiments which are observed connected with the incisors or the premolars, or do both conditions occur?

(3) Since in the Rodent series the number of the molars descends from 6 (in the upper jaw of *Lepus*) to 3 in the case of the Muridæ (in *Hydromys* even to 2), in forms with a reduced number a search would also have to be made for remnants of the molars which have been lost. It is clear that this task may partly coincide with one subdivison of the foregoing question (rudiment at the posterior end of the diastema). I wish to mention at once that in the present paper I have not devoted any special attention to this third question. Since the development of the molars in the Muridæ has been closely studied by Mahn under Fleischmann's direction, and since that author says nothing about rudiments of the vanished molars, which certainly would not have escaped his notice,

such an investigation seems at the very outset to offer but few prospects of success.

The material investigated by me is derived from embryos of *Lepus cuniculus*, *Sciurus vulgaris*, *Cavia cobaya*, *Cricetus frumentarius*, *Mus decumanus*, and *Mus musculus*. My methods consisted in the preparation of continuous series of sections through the heads of embryos according to well-known precepts. In particular I made use of the *technique* introduced by Prof. Born in the Breslau Anatomical Institute, as described by himself in his paper entitled "Noch einmal die Plattenmodellirmethode" *.

Plate-models were prepared of the most important stages. These naturally contained the epithelial tooth-rudiments, as well as the epithelium of the oral cavity from which they had proceeded; it is evident that Mahn (*loc. cit.*) worked in a precisely similar fashion.

I will take first the two species in the investigation of which positive results have been obtained, i. e. *Lepus* and *Sciurus*. The remaining forms, in which, in the sense of the queries which we have propounded, nothing was discovered, can subsequently be dismissed in a few words.

Lepus.

With reference to this form a series of statements are contained in Pouchet and Chabry's paper (*loc. cit.*), which it is necessary for me to cite, since I have partly to confirm, partly to amplify, and partly to refute them. The French authors confirm the older observations, that in the premaxilla of the Rabbit three larger incisors are formed on each side, which, however, do not stand side by side, but one behind the other. The second of the series are deciduous, and drop out shortly before or shortly after birth. The *i.* 3† are formed much

* Zeitschrift für wissenschaftliche Mikroskopie, Bd. v.: Braunschweig, 1888. In this paper Prof. Born writes as follows:—"As is well known, the essence of the plate-model method is that from each of a series of sections of equal thickness the parts which are to be modelled are drawn upon plates, which are exactly so much thicker than the section as the sketch is larger than the original. The parts drawn are cut out and stuck one upon another; in this manner a plastic reconstruction is obtained of the structure under investigation" (p. 445). .... "Formerly I scratched the outlines of the section upon prepared (cast) plates. I now use plates of waxed paper, in accordance with Strasser's suggestion, and after drawing upon the paper, I cause this to be thickened with wax until plates of the desired thickness are obtained" (p. 446).

† For convenience' sake here and subsequently *di.* 2 (according to the customary nomenclature) is designated shortly *i.* 2, while the permanent *i.* 2 is termed *i.* 3.

later than *i.* 1 and *i.* 2. From my own experience I have nothing to add to these statements, since the rudiment of *i.* 3 (the permanent *i.* 2) in the largest embryo examined by me (10 centim. in total length) was but little further developed than in the embryo from which fig. 20 of the French authors is derived. The rudiment of this tooth was represented by a clavate enamel-organ, indented only by quite a flat papilla, and situated ventrally and posteriorly to the greatly developed deciduous *i.* 2. As stated by Pouchet and Chabry, *i.* 2 and *i.* 3 lie in one and the same alveolus.

As Fleischmann convinced himself from the examination of transverse sections, the *di.* 2 are enamel-crowned teeth with two roots of dentine.

In the mandible the rudiment of only one large incisor is formed. In addition to this, however, Pouchet and Chabry discovered in *Lepus* two new deciduous teeth, which are situated in both jaws in front of the large *i.* 1. They found these teeth in embryos measuring from 28 to 45 millim. in length, and in a rudimentary condition, to which nothing analogous is known in other Vertebrates. The abridged account of their discovery runs somewhat as follows:—In embryos measuring from 28 to 45 millim. and something over in total length, there is found in front of the well-developed enamel-organ of the large incisor, and in direct connexion with its anterior face, an epithelial mass, which, in a cavity which is completely closed towards the exterior, contains a thimble-shaped cusp of dentine. The innermost columnar cells of the epithelial sac stand directly upon the surface of this cusp, and its pulp-cavity is filled with a certain number of blood-corpuscles and embryonic cells. The enamel-organ (for the epithelial sac can be considered as nothing else) of this dentine cusp is distinguished, according to the French authors, on the one hand by its compact texture (the enamel-pulp is absent), and on the other by the fact that it completely surrounds the cusp. The enamel-organ is connected by a cord of epithelium with the posterior side and the lower border of the sunken epithelial wall ("mur plongeant"). (Such is the term bestowed by these authors upon the sunken epithelial masses, which are found in many embryos in the region of the future groove between the lip and the alveolar margin. Projecting masses of epithelium, to which the authors apply the term "mur saillant," correspond approximately to the thickenings of the epithelium of the oral cavity at the edge of the jaw, which Germans call the jaw-wall [Kieferwall].)—Our cusp of dentine disappears long before birth, since it is either absorbed or drops out. According to Pouchet and

Chabry the enamel-organ of the large incisor is also connected by a cord of epithelium with the *mur plongeant*, but with its posterior and upper border. The authors referred to found a similar little rudimentary tooth in the upper jaw only in embryos which measured not less than 32 to 40 millim. in length. "It lies immediately in front of the large incisor, and its tip appears in the midst of the epithelium of the *mur plongeant*" (fig. 21).

The earliest stages which I was able to examine thoroughly consisted of embryos of *Lepus cuniculus* measuring 15 millim. in total length, of which the head occupied 9 millim. For earlier ones I had at my disposal only the series of sections from an embryo with a head 6 millim. in length. Since this shows only the dental fold, which is apparently continuous in the upper jaw, but in the lower one on the contrary is interrupted behind the region of the incisors, while the enamel-organs are as yet entirely absent, I shall defer the investigation of these youngest stages until I have more abundant material at my disposal.

First of all I deal with the region of the incisors in embryos with heads measuring somewhat more or somewhat less than 1 centim. The length of these embryos from the crown of the head to the root of the tail, which, for reasons which will be readily understood, is much more variable, fluctuates between 1·5 and 3 centim. Fig. 13 * gives a representation of the model which I have prepared of the epithelium of the oral cavity, with the tooth-rudiments of the upper jaw of the right side, of an embryo measuring ·9 centim. in cephalic length and 2·1 centim. in all; the model is seen from above and somewhat from outside; I have not figured a second model showing the rudiments of the incisors in the upper and lower jaws of an animal of about the same size.

In the lower jaw the rudimentary tooth discovered by Chabry and Pouchet may be seen. Fig. 1 gives a distinct view of this, from which it appears that the enamel-organ of the tooth is not closed on all sides, as asserted by Chabry and Pouchet, but is open on the underside. Through the aperture a richly nucleated pulp enters the interior of the tooth. The centre of the pulp is occupied by a wide blood-vessel, while its peripheral cells form a well-developed layer of odontoblasts, which has already secreted a solid hook-shaped cap of dentine. The latter, in the preparation upon which the drawing was based, has withdrawn a little from the well-developed enamel-epi-

* The figures referred to in this paper will be found in vol. 39 of the 'Archiv für mikroskopische Anatomie.'

thelium. In short, apart from the absence of enamel, it is a thoroughly typical representation of a small tooth-rudiment, such as we are otherwise wont to find in lower Vertebrates. The connective cord, which unites the enamel-organ of the rudimentary tooth with the epithelium of the oral cavity, actually extends with its anterior end, as stated by the French authors, as far as the posterior circumference of the *mur plongeant*, which is here but little developed. Further backwards, however, this connective cord proceeds, as is shown in fig. 1, from the unthickened epithelium of the oral cavity. Moreover, we see from the figure that a strong epithelial projection, which is directed inwards, starts from the spot where the connective cord passes into the actual enamel-bell (Schmelzglocke). This arrangement is repeated more or less decidedly in each section. According to the customary conception the tract α–β in fig. 1 would have to be regarded as the " dental fold " (" Zahnleiste "), on the outer side of which, close above the end without a neck, the enamel-organ of the rudimentary tooth would be situated. Whether this mode of interpretation is here correct, can only be determined by the study of younger stages, which I am reserving to myself. Now the enamel-organ of the large incisor of the lower jaw is directly connected with the posterior side of the enamel-organ of the rudimentary tooth ; in the same manner the cord which connects the enamel-organ of the rudimentary tooth with the epithelium of the oral cavity is posteriorly prolonged directly into the similar connective cord of the enamel-organ of the large incisor. If, as has been indicated above, we regard this cord as a dental fold, this continuity of the dental fold from one enamel-organ to the other would be nothing unusual, —on the contrary, it is in accordance with the general rule. The direct connexion, however, of two enamel-organs, as, moreover, also shown with great distinctness in fig. 19 (longitudinal section) of Pouchet and Chabry, is unusual. The enamel-organ of the permanent incisor is still at a very low stage of development. It is a lumpy epithelial mass, which on the posterior side appears somewhat flattened and indented. This shallow hollow subsequently deepens into the bell of the enamel-organ, which is open towards the rear. In the rudiment of the large incisor no trace of tooth-substance is yet developed.

Behind the large incisor the dental fold in the lower jaw entirely ceases. In order to dispose of this question at once, it may be mentioned that in the case of *Lepus*, in this, as in all subsequent stages, an absolute diastema is found in the

lower jaw between the incisor and the molars, in which distinct vestiges of a dental fold can never be detected.

Now as regards the incisors of the premaxilla in rabbit-embryos of about 1 centim. in cephalic length (*cf.* fig. 13): contrary to the statements of Chabry and Pouchet, the rudimentary tooth in the premaxilla is also already completely developed in embryos measuring 1 centim. in cephalic length, and about 2 centim. in all. As is shown in fig. 13, it is situated upon the epithelium of the oral cavity close behind the *mur plongeant*, which is still but little developed, in such a manner that a special connective cord between its enamel-organ and the oral epithelium cannot be distinguished. The enamel-organ is longer than in the lower jaw; the longitudinal axis appears to be directed obliquely upwards and outwards. At the upper end, displaced a little towards the front, we find the very narrow aperture, surrounded by a swollen margin, which leads into the interior of the pulp-cavity. The solid dentine tooth is developed just as beautifully as in the lower jaw. Owing to the absence of a special connective cord, the rounded tip of the very long tooth is separated from the surface of the epithelium of the oral cavity only by a few layers of cells. In the upper jaw also the enamel-organ of the rudimentary tooth is in direct continuity with that of the large incisor. In the model it is easy to recognize the peculiar conditions which are presented by the attachment of the first large incisor to the epithelium of the oral cavity,—conditions which can hardly be understood from the examination of sections, and to which it is only with difficulty that justice can be done in description also (in the figure, too, they can be seen but imperfectly). For behind the spot at which the enamel-organ of the large incisor is attached, the roof of the oral cavity bulges out downwards in the form of a step. (A similar step follows further back at the spot at which the enamel-organ of *i.* 2 is attached.) Moreover, the connective cord of the enamel-organ of the large incisor has a peculiar shape; for it consists of two plates, one placed transversely, the front of which, like the greater portion of the enamel-organ itself of *i.* 1, is fused with the enamel-organ of the rudimentary tooth, and another in the shape of a sagittal plate, attached at right angles to the inner edge of the former, and prolonged backwards as far as the enamel-organ of *i.* 2. In the case of the latter tooth the same conditions are repeated. We can also express the facts by saying that the connective cords, which unite the enamel-organs of *i.* 1 and *i.* 2 with the epithelium of the oral cavity, are hollowed out from behind and somewhat from inside. The connective cord of the first incisor is

fused in front with the enamel-organ of the rudimentary tooth, and behind passes into the connective cord of *i.* 2, while, as we shall see, the latter is prolonged backwards into the dental fold of the diastema. This, together with the steps, produces, as has already been stated, highly complicated appearances. What we have to remember is, that the enamel-organs of *i.* 1 and the rudimentary tooth are in direct continuity, while *i.* 1 and *i.* 2 are united by a structure which may well be regarded as a dental fold. The epithelial mass of the enamel-organ of *i.* 1 itself is lumpy, and when seen from the upper side behind somewhat flattened and indented. The margins of this hollow subsequently become more decidedly elevated, and so assume the characteristic bell-shape. The enamel-organ of *i.* 2 is, as may be seen from fig. 13, in not nearly so developed a condition.

We will here at once mention the changes which take place in the region of the incisors in subsequent stages. With reference to the lower jaw we have to observe that the sunken epithelial wall (*mur plongeant*), which marks out the subsequent groove between the lip and the alveolar border, becomes much more strongly developed and extends further backwards. In the foremost sections it appears as a bifurcate and deeply sunken epithelial mass, which to a certain extent ensheaths the anterior end of the Meckelian cartilage and the covering bones lying thereon. On the inside of the epithelial mass is attached the common connective cord of the enamel-organs of the rudimentary tooth and of the large incisor. The latter in embryos measuring 1·5 centim. in cephalic length and about 4 centim. from crown to rump, already assumes the well-known bell-shape, in the manner which has been indicated above. Since the size of this bell, which is enormously expanded behind, and within which the tooth develops in the usual way, by far preponderates, it now appears as though the tip of the rudimentary tooth were implanted in the cord connecting this great bell with the epithelium of the oral cavity, while only the lower end of the tooth, surrounded by its enamel-organ, projects freely downwards in front of the great bell. The conditions which are now present are consequently similar to those which are shown in fig. 14 in the case of the squirrel. The rudimentary tooth is indeed far behind the large incisor in growth, but nevertheless in older animals, *e. g.* in rabbits measuring about 2·5 centim. in cephalic length and *circa* 7 centim. in all, it has decidedly increased in size in comparison with the younger stages. Its pulp-cavity is never closed towards the exterior, as is stated by Chabry and Pouchet, but always remains in connexion

with the surrounding mesoderm, though it is true not in the simple manner which is seen in fig. 1. In larger rabbits the size of the rudimentary tooth appears decidedly diminished, as though it were in process of absorption. In still later stages I could no longer find any trace of it, although I am unable to make any precise statement as to the manner of its disappearance, any more than Chabry and Pouchet were able to do.

In the premaxilla the changes are precisely similar to those in the lower jaw. A strong sunken epithelial wall is formed, which indicates the region of the subsequent cleft between the two halves of the lip and the anterior end of the jaw. It consequently appears simple in the foremost sections, and bifurcate further back. One half of it is to be seen in fig. 2, and a longitudinal section in the combination-picture shown in fig. 3. In this enormous epithelial mass the anterior step on the roof of the oral cavity, as described above in the younger stage, completely disappears. On the inside of the lateral tip of this epithelial mass is situated, as is shown in fig. 2, the enamel-organ of the rudimentary tooth (fig. 2 belonged to a series through the head of a rabbit embryo measuring 5·1 centim. in all and 2·3 centim. in cephalic length). The enamel-organ of the first incisor develops into a huge bell, which is open behind, and, in accordance with the conditions previously described (*cf.* figs. 2 and 13), the rudimentary tooth now appears to lie in the cord connecting this bell with the *mur plongeant*. Owing to the development of the *mur plongeant* the tip of the tooth has naturally penetrated very deep down. The combination-picture fig. 3, which is constructed from longitudinal sections through the head of a rabbit embryo of the same size as that of fig. 2, shows these conditions perhaps most distinctly.

The histological conditions of the rudimentary tooth may be recognized in fig. 2; its dentine casing appears broken through on the outside in this figure. The connexion between the pulp and the mesoderm takes place through this breach, not directly however, but in a very complicated fashion, since the enamel-organ appears as if cleft by strands of connective tissue, producing conditions of which the detailed description belongs to another place. In the same way I have no intention of entering into a discussion of the histological conditions in the enamel-organ of the large incisor. I would merely refer the reader once more to fig. 2, which in some degree exhibits the peculiar penetration of vascular outgrowths into the outer wall of the enamel-organ, which has already been dealt with by so many investigators. The rudimentary tooth

of the premaxilla persists for about as long as that of the lower jaw. I am at present unable to say anything as to the manner of its disappearance. In embryos with a cephalic length of 1·7 centim., and measuring 4·5 centim. in all, the dental fold between the first and second incisors was still present, although it is true that its connexion with the oral epithelium had almost everywhere disappeared. The enamel-organ of *i.* 2 had become distinctly campanulate. In an older series the dental fold between the two large incisors had already entirely disappeared, although in the model of the stage in question the step upon the palate was still to be seen, to the anterior margin of which the cord connecting the enamel-organ of *i.* 2 with the oral cavity was previously attached, while, in all probability as a remnant of this connexion, we still find an epithelial projection jutting out slightly into the connective tissue.

While up to this point, with the exception of immaterial modifications, I was able to confirm the statements of Chabry and Pouchet on the subject of the development of the teeth in the rabbit, the results at which I have arrived with reference to the diastema in the upper jaw are quite different from those obtained by the French authors. The latter assert that in the rabbit the dental fold is entirely interrupted in the diastema in both jaws. As I have already mentioned, I can confirm this statement as regards the lower jaw. In the upper jaw, on the contrary, I find the dental fold already typically developed, in the youngest stages investigated by me (measuring about 1 centim. in cephalic length and from 2 to 3 centim. in all), throughout the entire length of the diastema between the rudiments of the incisors and those of the molars. A good representation of this is given in fig. 13. The dental fold is situated in precisely the same spot as that in which it is found in mammals with a complete dentition, *i. e.* internally to the furrow made by the approximately horizontal roof of the mouth in bending round into the perpendicular mucous membrane of the cheeks. The spot at which the dental fold is attached is in the region of the diastema, as in that of the rudiments of the molars, somewhat depressed, towards a protuberance of the surface of the palate situated on the inner side of it (jaw-wall?). It is perhaps expedient, in addition to the measurements, to give yet other characteristics of the stage in which the fold is found to be fully developed. The stage is that in which the closure of the palate has just been completed, in which we still find distinct remains of epithelium in the perpendicular palatal suture, and in which, in the horizontal palatal suture (between the nasal

septum and the hard palate), a characteristic arrangement of the connective-tissue elements is still evident; by this, however, it is in no way intended to imply that the epithelial fold is not already present before this stage when the palatal cleft is open, and subsequently when the palatal suture has disappeared. My series furnish me with sufficient proofs of both cases. I merely wished to characterize the stage at which the fold appeared to me to be most developed. The epithelial fold at its anterior commencement is very shallow and inconspicuous, as it is also reproduced in model 1, and is connected with the enamel-organ of *i.* 2. In the region of Stenson's canal it is sometimes so inconsiderable that it is with difficulty detected. Behind this it speedily increases in height, and attains its greatest elevation at the transition into the rudiments of the molars. In the sections it appears as an epithelial cord, which proceeds from the epithelium of the oral cavity, inclined somewhat obliquely inwards, and is buried in the mesoderm. In the neighbourhood of the oral epithelium it appears narrow, having a breadth of only two very low rows of cells; the sunken end is thickened into a button-shape, owing partly to the increased height of the peripheral cells and partly to the intercalation of several cells in its interior. The form and size naturally vary very considerably according to the direction of the section and other accidental circumstances. Fig. 4 gives a representation of the epithelial fold in a series in which it appears particularly broad. In the other series it looks decidedly more slender and longer. In the section figured (fig. 4) the length of the epithelial depression amounts to about 100 μ, the breadth of the thick end to about 60 μ, and that of the narrowed neck to 30 μ. In the series from which the model shown in fig. 13 is constructed, the height of the epithelial fold at about the middle of its length amounts to nearly 120 μ, the breadth at the thickened end only to something over 20 μ, and at the narrowed neck only to about 10 μ.

Even in an embryo measuring 11 millim. in cephalic length and 34 millim. in all, but much more distinctly and much more extensively in an older one of 17 millim. and 44 millim. respectively, the dental fold in the diastema exhibits a remarkable modification. At first only for a limited space, but in the older embryo almost throughout its entire length, the neck of the epithelial fold appears broken through by the mesoderm. The appearances in this connexion are precisely similar to those seen in other places, where a strand of epithelium is displaced by the adjacent connective tissue. The breach sometimes affects only the portion beneath the button-shaped

end, so that a small cone is attached to the oral epithelium, followed by connective tissue, in the arrangement of the cells of which we can still frequently trace the direction of the epithelial cord which has disappeared. Deep down we then see the severed thickened end as a circle filled with epithelial cells, which is distinguished by the fact that, like other epithelial remnants undergoing degeneration in the same way, it takes up carmine very freely, and consequently appears of a dark red colour. It is clear that this process is the same as that also undergone by the dental fold in mammals with a complete dentition, after the enamel-organs have been formed and constricted off from it. The dental fold in the diastema of the rabbit, however, perishes without ever having produced enamel-organs. In an embryo rabbit 23 millim. in cephalic and 51 millim. in total length every trace of the fold has disappeared in the anterior portion of the diastema; but in the posterior portion, on the contrary, in the neighbourhood of the molars, there appears in each section at the same spot in the connective tissue of the palate a small red circle, which I am inclined to regard as the last vestige of the dental fold. My reasons for doing so are the following:—In the first place, it is found in the posterior portion of the diastema in every section at the same spot, and this spot, so far as I can see, corresponds to that at which the epithelial fold is found in younger stages. Secondly, in the connective tissue there frequently proceeds from the red spot to the oral epithelium a kind of cord of cicatricial tissue, *i. e.* a clear streak, in which we find but few nuclei, or none at all, while at the edges of it the nuclei are closely packed. Thirdly, the epithelial circle can be traced as far as the dental fold of the first premolar, though I am unable to assert with absolute certainty that a direct connexion exists. If my interpretation is correct, it would result therefrom, that the dental fold in the diastema in the rabbit disappears from in front backwards.

With regard to the rudiments of the molars in *Lepus cuniculus*, I have no special statement to make. In fig. 13 we see only three, and these still in a very undeveloped condition: the enamel-organs have the shape of flat shells. Another model, which is not figured here (prepared from a series of longitudinal sections through the head of a rabbit embryo 2·3 centim. in cephalic and 5·1 centim. in total length), shows the rudiments of five molars. In the second and third we find the characteristic bell-shape, with the projections directed towards the pulp. Nos. 1 and 4 are less developed; the fifth rudiment appears in the form of a button-shaped epithelial thickening, with only quite a shallow depression, at the posterior end of the dental fold.

Sciurus.

Of this very interesting form, as it proved to be, I succeeded, in spite of a considerable expenditure of trouble and expense, only in obtaining one pregnant female with seven embryos. However, I reserve to myself the working out of older and younger stages, since I have at any rate learnt the way in which these may be obtained with certainty next year. Fortunately the stage which I have before me corresponds fairly accurately with that to which the most important statements of Chabry and Pouchet refer. Since I differ from them very considerably, it will be well to give a summary of the statements of the French authors, which are somewhat difficult to understand. They run as follows :—" The dental fold commences in the upper jaw at the level of the incisors, and extends to beyond the molars. . . . In front of the canals of Stenson the dental fold is entirely wanting. . . . In the mandible the dental fold is continuous throughout the entire extent of the diastema."

Now follows a sentence which does not seem quite intelligible after what has gone before. It runs :—" Consequently the dental fold in all Rodents which we have studied is composed of two halves, which are not united in the middle. In the squirrel in particular the incisors arise from the same epithelial invagination (involution) as the molars."

According to what was previously stated, this would be correct only for the lower jaw. For in the upper jaw the dental fold is said to be completely wanting even before the canals of Stenson.

The explanation of the figures shows that the statements of Chabry and Pouchet refer to embryos of the length of 4 centim. The embryos studied by me were 2 centim. in cephalic length and 4·7 centim. in all, and were consequently only slightly larger than those examined by the French authors.

The following are the results which I obtained :—

(1) Like the rabbit, the squirrel possesses in front of the large incisor a rudimentary tooth, which seems to have been overlooked by Chabry and Pouchet.

(2) There is found in the lower jaw, in the diastema between the incisors and molars, and extending only for a very short space, about as far as may be seen in fig. 15, in continuation of the dental fold of the incisors, a small epithelial cord, which is detached from the epithelium of the oral cavity, and is to be regarded as a remnant of the dental fold. In the whole of the large space behind this, as far as the molars, no

trace of it can be detected. Whether we may assume that in the only slightly younger stages which were investigated by Chabry and Pouchet, a complete dental fold is, as stated by these authors, present throughout the entire diastema of the lower jaw, is a question which I must postpone until I have more ample material at my disposal. I do not think it probable that it is so.

(3) In the upper jaw very extensive remnants of the dental fold are found in the diastema. The fold is not once wanting in any section from the incisor to Stenson's canal: compare figs. 8–10, and the model (fig. 14). In most places the epithelial cord is detached from the epithelium of the oral cavity, in others it is connected with it. It frequently appears to lie parallel to the surface of the palate; the nuclei of the connective tissue are disposed in a regular concentric arrangement around the epithelial remnant. This is therefore directly contrary to what is stated by Chabry and Pouchet.

Behind the orifice of Stenson's canals we find for a space no vestige of the epithelial fold: then it is present in certain sections once more, or in its place there appears a kind of cicatrix in the connective tissue. Even before the middle of the space between the orifices of the canals of Stenson and the first molar, we observe a remnant of the epithelial fold as an element which is again regularly visible in every section. At the posterior end it is easy to distinguish the way in which this remnant of the dental fold of the diastema passes into the dental fold of the first molar. It may further be remarked that in this tract also there is much variation; for the epithelial cord may appear larger or smaller, perpendicular or bent round, connected with the epithelium of the oral cavity or isolated. After this discovery it appears scarcely open to doubt, that in younger stages of *Sciurus* the diastema in the upper jaw is traversed by a continuous dental fold, precisely as in the case of *Lepus*.

(4) On the outer side of the dental fold in the diastema there are situated two little enamel-organs with distinct papillæ,—one close in front of, and the other in the plane of a transverse section through, the orifices of the canals of Stenson (*cf.* model, fig. 14). These two enamel-organs naturally lie one close behind the other. In both the aperture of the enamel-bell is directed forwards and upwards. The anterior of these two enamel-organs is the better characterized as such, in that it contains enamel-pulp (*cf.* fig. 7). But that the posterior rudiment is also of the nature of an enamel-germ (*cf.* fig. 10) is scarcely open to doubt. It is curious that in their fig. 26, MM. Chabry and Pouchet have given a perfectly

characteristic representation of the posterior of the two rudiments (the section also passes through the region of the orifice of the Stenson's canal): compare for this purpose my fig. 10. But according to the explanation of the figures they interpret the rudiment quite wrongly as that of the large incisor, which, as a glance at the model, fig. 14, will show, is much further developed, and besides this also has quite a different position.

It now remains for us to make more special observations with reference to certain of the above four paragraphs.

The dental fold upon which in the lower jaw the enamel-organs of the rudimentary tooth and of the large incisor are situated (*cf.* for this figs. 5 & 6, and model, fig. 15) proceeds from the commencement of a peculiar *mur plongeant*, which envelops as a deep case the anterior end of the Meckelian cartilage together with the superincumbent covering-bone. It is precisely the same formation as that described and figured by Chabry and Pouchet for the rat. Together with the epithelium of the oral cavity, it appears in a median transverse section as a closed circular epithelial arch, in the interior of which the dental rudiments, the bone, and the cartilage are contained. Upon the surface of the mucous membrane of the oral cavity, the spot from which the epithelial fold and beside it the *mur plongeant* proceed is distinguished by a groove. For posteriorly the epithelial fold ceases to be in continuity with the epithelium of the oral cavity (*cf.* model, fig. 15). That from the fold an epithelial cord runs backwards for a short distance has already been mentioned, and may be seen from the model. Now on the outer side of this epithelial fold the enamel-organs of the rudimentary tooth and of the large incisor are attached close together, each by means of a long neck, in such a way that only the somewhat clavate end of the epithelial fold projects a little further downwards and inwards than this point of attachment. For, as is shown both by the figures and the model, the neck of the rudimentary tooth is a particularly elongated structure, which reaches so far downwards and backwards, that the enamel-bell of the rudimentary tooth comes to lie beside the Meckelian cartilage (*cf.* fig. 6). Neither the neck of this enamel-organ, the stouter and more massive one of the incisor lying behind it, nor lastly also the dental fold itself have smooth outlines; on the contrary, they are beset with projections and depressions of the most varied kind (*cf.* for this figs. 5 & 6), so that in many places the appearance presented reminds us of that of the proliferating rudiment of a gland, or still better of that of a carcinoma.

The opening of the enamel-bell of the rudimentary tooth is, like that of the large incisor, directed backwards. Within it we do not find, as in the case of *Lepus*, a well-formed tooth of dentine, but a small, inconsiderable, almost solid dentine cusp, into which from the inner side only a narrow cord of connective tissue enters. This cusp, too, appears to be no longer enveloped on all sides by epithelium. With reference to the neck of the enamel-organ of the incisor, which follows after it, there is nothing more to be said than that at its starting-point from the dental fold it is broadly fused with the neck of the enamel-germ of the rudimentary tooth.

The position of the germ of the rudiment in the upper jaw is explained by model fig. 14. We observe that it is situated in front of the enamel-germ of the large incisor. The enamel-germ of the rudimentary tooth of the upper jaw is likewise attached to a long neck, which passes obliquely upwards and unites with the massive neck of the large incisor of the pre-maxilla. Here also, though certainly less decidedly than in the lower jaw, the irregularity of contour is repeated. The opening of the enamel-bell of the rudimentary tooth is directed backwards and upwards. Inside it the pulp surrounds a delicate little cap of dentine. Figs. 11 and 12 will explain these statements. Fig. 11 gives a representation of the arrangement magnified nearly fifty times. We see from the figure that the enamel-germ of the rudimentary tooth and that of the large incisor are surrounded by one and the same thickened envelope of connective tissue. Fig. 12 shows from the same section the enamel-germ of the rudimentary tooth magnified nearly two hundred times.

With reference to paragraph no. 4 the following remarks must be made :—Fig. 7 shows, magnified one hundred times, a section through the anterior rudimentary enamel-organ, which is situated close in front of the orifice of Stenson's canal. We also get a sectional view of the portion of the dental fold belonging to it; but in this section the fold is in connexion neither with the epithelium of the oral cavity nor with the transversely-directed neck of the enamel-organ. Both, however, lie together in an envelope of connective tissue, which is packed with nuclei and consists of concentric layers. In the interior of the enamel-bell distinct enamel-pulp is found: a dentine germ could not be distinguished. The most superficial nuclei of the pulp appeared clearer: this is somewhat exaggerated in the figure. They were separated from the deeper-lying dark ones by a transverse cleft, which perhaps represents a blood-vessel.

Fig. 8 shows the arrangement of the structures, magnified

twenty-six times, about nine sections (15 μ) further back. The section passes through the anterior circumference of the orifices of Stenson's canals. Of the enamel-bell of the anterior rudiment only the posterior margin is still cut, while inwards from it is seen the dental fold detached from the epithelium.

Fig. 9 lies three sections further backwards (same scale). The section passes through the narrow interval between the two rudimentary enamel-organs. The dental fold is to be observed, and to the side of it a thickening of the epithelium of the oral cavity, with which the fold at other spots is connected. Lastly, fig. 10 lies only two sections behind the foregoing, and shows the second rudimentary enamel-bell. This is by far less distinctly characterized as such than is the former one. For, in the first place, it is directly attached to the outside of the epithelial fold, and is united to the epithelium of the oral cavity by means of a short thick connective cord. Secondly, the enamel-pulp is absent from its interior, and, moreover, the connective-tissue-pulp, or tooth-papilla, is not so thickly nucleated as in the case of the anterior rudiment. Yet the whole structure is enveloped in a concentric membrane of connective tissue (not visible in the figure), and, especially after examination of the model, fig. 14, it is hardly possible to doubt that the rudiment is of the nature of an enamel-organ.

Cavia.

Of *Cavia* I was able to examine a small specimen of the cephalic length of 4·5 millim. This presented no special interest for our subject, since the tooth-rudiments were still at the very commencement of their development*.

Then come two series, one through the head of an embryo measuring 1·4 centim. in cephalic length and 2·9 centim. in all, while the other was derived from a somewhat younger specimen, which Prof. Froriep, of Tübingen, was kind enough to make over to me. The stages were so far very favourable in that they corresponded to those of the rabbit in which the rudimentary tooth-germs are most distinct. The result of the investigation was, however, an almost negative one: no trace of a rudimentary tooth and no trace of a germ for the second incisor. In the diastema there were found here and there thick cones of epithelium, which projected downwards for a

* I am indebted for this specimen to the kindness of Dr. Keibel, of Freiburg i. B., who placed at my disposal a whole series of guinea-pig embryos. Most of these, however, were too young and consequently not available for the purposes of my investigation.

certain distance from the epithelium of the upper jaw, and were also frequently continued backwards through a few sections as detached round epithelial circles, after which, however, they always came to an end. It is very possible that these represent remnants of the dental fold, though it is true that a more definite proof cannot be advanced. We might do this if we could trace such an epithelial cone into continuity either with the dental fold of the incisors in front, or with that of the molars behind. But we can do neither. Yet one argument which supports the idea that these cones are of the nature of a dental fold is to be found in the place from which the ingrowths start, which agrees fairly well with the typical position of the dental fold in *Lepus*. It is true that in *Cavia* the relations of the epithelium of the oral cavity and of the mucous membrane of the palate are somewhat different from those in *Lepus*; but this is a question which I cannot here proceed to discuss. Moreover we might establish a proof by the process of exclusion; besides rudiments of a dental fold, the epithelial cones could only be germs of glands. It is, however, improbable that the germs of small oral pituitary glands would be already so distinct in the stage which we are considering. But this attempt at a proof is not sufficient.

Cricetus frumentarius, Mus musculus, *and* Mus decumanus.

Few words are needed to dispose of these animals. Although we had at our disposal continuous series of at least the two last-named species, the investigation of them nevertheless produced absolutely negative results. Not a trace of rudimentary tooth-germs was found either in the neighbourhood of the incisors or in the diastema.

The discussion and valuation of my results may be divided into heads according to the questions with which we started:—

(1) Are embryonic tooth-rudiments found in the neighbourhood of the incisors in Rodents? To this we reply:—In *Lepus* we find a rudimentary tooth in the upper and lower jaw in front of the large incisor, as already discovered by Chabry and Pouchet. This remarkable observation appears to have escaped the notice of most of the subsequent authors, but I was able to confirm it and to add that evidently the same tooth-rudiment is also present in the squirrel.

Now Dr. Fleischmann has led me to inquire whether this rudimentary tooth represents the remnant of an *i.* 1—in which case the large incisor would have to be designated *i.* 2, which

agrees in a remarkable manner with Cope's derivation of the Rodents, as quoted above,—or whether it must be considered as the remnant of the germ of a precursor of the large incisor. Unfortunately the material furnished by the actual results does not entirely suffice for a decision between these two alternatives.

The development of the rudimentary tooth, as I was able to follow it continuously in *Lepus*, by no means agrees in its main features with that of a milk-tooth, whether, in respect of the relation between the development of a milk-tooth and that of the permanent one, we accept the older view, which is reproduced in the text-books, or that which is held by Baume. So far as I am aware, no case is known in which the enamel-organ of a milk-tooth appears directly united with that of its successor, as MM. Chabry and Pouchet have already shown to be the case in *Lepus*, at least with regard to the rudimentary tooth of the lower jaw. In the premaxilla the French authors failed to observe the stage in question; I was able to show that here, at any rate at first, the same thing takes place in *Lepus*.

In a superficial examination of the question, the conditions pertaining to the second deciduous incisor in the premaxilla of *Lepus* tell very much against the assumption that the rudimentary tooth likewise belongs to the milk series. The deciduous incisor referred to is clearly a true precursor of the second and smaller permanent incisor. It attains a high degree of development at a time when the germ of the permanent *i.* 2, which at all events proceeds from the adjoining portion of the dental fold, is still quite small and insignificant. It is not until the last stage of fœtal life that the permanent *i.* 2 becomes more strongly developed and displaces the deciduous *i.* 2, which drops out shortly before or after birth.

Now are we to suppose that in *Lepus* the second incisor has retained a true milk-tooth as its precursor, while in the case of the first incisor the milk-tooth remains in quite a rudimentary condition, and is outstripped unusually quickly by the germ of the permanent tooth, which appears at the same time as, or even earlier than, that of *di.* 2? It is true that in explanation of this divergence we can adduce the necessity for a more speedy development of the permanent *i.* 1 (which, indeed, represents the actual large incisor), whereby to a certain extent its precursor is deprived of the necessary material for development, and is prevented from passing beyond a rudimentary condition.

Finally, we must also confess that it is more easily imaginable that the enamel-organs of a milk-tooth and its

successor, which in some other way at any rate also stand in closer relation one to another, should under the special conditions in question (especially great and therefore also more rapid development of the permanent tooth) fuse together, than that two tooth-germs situated one behind the other, which have otherwise nothing whatever to do with one another, should enter into intimate mutual relations of this kind. Another telling point is that the rudimentary tooth and the incisor lie together not only in an alveolus, but also, as may be seen with especial distinctness in the case of the squirrel, in one tooth-sac of connective tissue. I do not wish to attach too great weight to the relative position of the tooth-germs. It is true that the rudimentary tooth lies in front of the incisor, but the deciduous *i.* 2, which we must yet certainly regard as a milk-tooth, also lies, at least according to the representation of MM. Chabry and Pouchet, in front of the germ of the second permanent tooth. This is connected with the peculiar conditions of space in the jaws of Rodents. It appears to me to be of more importance that in the squirrel, in which the conditions in question seem to be to a certain extent less abnormal than in the rabbit, the enamel-germs of the rudimentary and permanent tooth are connected together by their "necks" (and this both in the upper as well as in the lower jaw) precisely as this is usually described for the milk-tooth and its successor. Altogether I am personally more inclined to the view that *the rudimentary tooth is to be considered as the rudiment of a precursor of the large incisor in process of active degeneration*, though I am ready to admit that this can by no means be regarded as finally established. It may further be specially pointed out that in *Sciurus*, which in many respects has proved even more conservative than *Lepus*, no distinct trace could be discovered of *i.* 2, which *Lepus* has preserved in the shape of the milk-tooth and its successor. It will be shown later on that the anterior of the two enamel-organs, which I have proved to exist near the orifices of Stenson's canals, can only with difficulty be regarded as *i.* 2. Further investigations will have to determine whether the rudimentary teeth, as they appear in the stage of *Sciurus* examined by me, have exactly arrived at the height of their development, whether they develop still further, or, lastly, whether they are not perhaps already in process of degeneration.

(2) In the Rodents examined are germs of teeth found in the diastema? To this our discoveries enable us to reply:— In *Lepus* a well-developed dental fold is found throughout the

entire length of the diastema, but only in the upper jaw, which was expressly denied by Pouchet and Chabry.

Upon this dental fold, however, enamel-organs are never developed in *Lepus*. After having lasted for a somewhat lengthy period, it disappears without leaving a trace behind.

In the upper jaw of *Sciurus* in the stage we examined a dental fold was present, which was interrupted for a certain distance behind the canals of Stenson, but was otherwise greatly extended and continuous. According to Chabry and Pouchet it is just in front of Stenson's canals that the fold is wanting. Moreover it is asserted by the French authors, though their statements upon this point are certainly somewhat confused, that in the lower jaw there is a complete dental fold throughout the entire diastema. In our stage, which was but a little older, it was possible to distinguish mere traces of a prolongation of the dental fold close behind the rudiment of the incisor in the lower jaw, so that the statement of MM. Chabry and Pouchet does not appear to me to be a very credible one. On the other hand, we may with confidence assume that in younger stages of the squirrel the dental fold of the upper jaw will be found perfectly continuous in the diastema.

In addition to this we find in *Sciurus* near the canals of Stenson two enamel-organs lying one close behind the other, of which the anterior is quite undeniably characterized as such, while the posterior bears somewhat less distinct, but nevertheless sufficiently definite, indications of its character. It is remarkable that Chabry and Pouchet have figured one of these rudiments, but, as we have seen, have interpreted it quite incorrectly.

How are these structures to be regarded? The anterior enamel-organ can scarcely be regarded as a remnant of the *i.* 2 which is present in *Lepus*; for in this animal the cord connecting *i.* 2 with the epithelium of the oral cavity is attached far in front of the orifices of Stenson's canals; the interval which is visible in fig. 14 (of the squirrel) between this rudiment and that of *i.* 1 appears much too great for it to be possible to assume that we are here dealing with two tooth-rudiments following directly one after the other. It is true that this question too will not be finally decided until we have examined younger stages, since the possibility of a secondary divergence of the two rudiments is also not excluded, although it is not probable that this has taken place. Moreover it will be determined only by further investigations whether a deposition of dentine still takes place in these

rudiments or not, and how they disappear. Taking the conditions as we find them in the stage under consideration, we might regard these two enamel-organs as remnants of rudiments of a posterior incisor and a canine tooth which have been strangely preserved; their interpretation as remnants of premolars is opposed by their position beside the orifices of Stenson's canals.

The reader may here once more be reminded that in *Cavia* only very doubtful remnants of the dental fold were distinguishable in the diastema, while in *Cricetus* and *Mus* no trace of a rudimentary embryonic dental germ was visible.

In conclusion, it may be also pointed out that our results correspond to Fleischmann's view, according to which the degeneration of the tooth-rudiments has advanced further in the lower than in the upper jaw. Apart from the doubtful statements of MM. Chabry and Pouchet with regard to the squirrel, no dental fold was found in the diastema in the lower jaw; in the upper jaw, on the other hand, a structure of this kind was distinguishable in a condition of greater or less completeness in *Lepus*, *Cavia*, and *Sciurus*, while in the case of the last-mentioned form it is even provided with enamel-organs. It also agrees very well with the general views of Schlosser and Fleischmann, that the Lagomorpha represent an especially old and conservative Rodent type, and that after these the Sciuromorpha come next in order; that in representatives of these groups it was possible to demonstrate the most distinct and most widely extended embryonic remains of tooth-rudiments which have disappeared; while in the more highly modified Myomorpha, in so far as these were investigated, the embryonic reduction was also more complete. Lastly, stress may likewise be laid upon the fact that the discovery of a dental fold in the diastema in the case of *Lepus* and *Sciurus* is in conformity with the similar discoveries of other authors in the case of different Mammals with incomplete dentitions. Thus the presence of a dental fold in the diastema in the premaxilla of Ruminantia was not long since finally determined by Mayo *. For the Edentata the same was proved by Chabry and Pouchet, and it is well known that in the case of the whalebone whales Geoffroy St.-Hilaire has demonstrated the existence not only of the dental fold, but even of entire embryonic teeth, which merely fail to cut the gum and are absorbed within the jaw.

* Mayo, "The Superior Incisors and Canine Teeth of Sheep" (two plates), 'Bulletin of the Museum of Comparative Zoology at Harvard College,' vol. viii. (Cambridge, 1886-1888).

At the end of my paper I will add a few words of thanks.

In the first place, I am most deeply indebted to Prof. G. Born, Prosector to the Royal Anatomical School of Breslau and Director of the Embryological Section. It was he who first induced me to undertake these exceedingly interesting and instructive studies, he initiated me into the always difficult *technique* which work of this kind demands, and he assisted me by word and deed wherever he could, shunning no trouble and no expense. In return for his extraordinary amiability and self-sacrificing care I trust I may be permitted once more to express here my heartiest thanks to Prof. Born.

I am likewise under very special obligations to Prof. Hasse, Director of the Royal Anatomical School of Breslau, for the permission which he most readily accorded to me to work in the Embryological Laboratory of the School.

Lastly, my best thanks are due to Dr. A. Fleischmann, of Erlangen, who drew my attention to a series of highly remarkable facts, introduced me to the palæontological literature of the subject, and furnished me with very valuable statements and observations for my memoir.

LIII.—*On the Habits of a Species of* Trigona.

By J. H. Hart, F.L.S., Royal Botanic Gardens, Trinidad.

Among the several species of *Trigona*, or "wild bees," which are common in Trinidad none is more interesting in its habits than a peculiar small dark species which is often found in the proximity of dwelling-houses, under slates, or in crevices of the woodwork of out-buildings.

The specific name of the insect has not been ascertained, but it has been found that it belongs to the genus *Trigona*. It was first observed in 1887 in the walls of a dwelling-house, owing to its building a peculiar entrance-tube. This tube was about $\frac{3}{4}$ of an inch in diameter, about 4 inches long, with the entrance at the bottom, through a small hole in the centre of the wax disk which closes it.

When the office of the Royal Botanic Gardens was under repair quite recently the same species was discovered making its home between two walls.

An attempt was made to house them, and a small box prepared, with a small cut for entrance allowed, in a similar manner to that usually seen in the common bee-hive, viz. at the base. The bees took to the box and commenced work;